

Title Page

**The contribution of mosses to the carbon and water exchange of arctic ecosystems:
quantification and relationships with system properties.**

J.C. Douma¹, M.T. van Wijk^{1,*} S.I. Lang³ and G.R. Shaver²

¹ Wageningen University and Research Centre, Plant Production Systems, Plant Sciences,
Wageningen, The Netherlands

² The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA

³ Vrije Universiteit Amsterdam, Systems Ecology, Amsterdam, The Netherlands

* Corresponding author:

Email: mark.vanwijk@wur.nl

Telephone: (+)31 - (0)317-486102

Fax: +31 - (0)317-484892

Address: Plant Production Systems, Plant Sciences,
Wageningen University and Research Centre
P.O. Box 430
6700 AK Wageningen
The Netherlands

Running title: carbon and water exchange of arctic mosses

Abstract

Water vapour and CO₂ exchange were measured in moss dominated vegetation using a gas analyzer and a 1 m by 1 m chamber at 17 sites near Abisko, Northern Sweden and 21 sites near Longyearbyen, Svalbard, to quantify the contribution of mosses to ecosystem level fluxes. With the help of a simple light-response model we showed that the moss contribution to ecosystem carbon uptake varied between 14 and 96%, with an average contribution of around 60%. This moss contribution could be related to the NDVI (normalized difference vegetation index) of the vegetation and the leaf area index (LAI) of the vascular plants. NDVI was a good predictor of gross primary production (GPP) of mosses and of the whole ecosystem, across different moss species, vegetation types and two different latitudes. NDVI was also correlated with thickness of the active green moss layer. Mosses played an important role in water exchange. They are expected to be most important to gas exchange during spring when leaves are not fully developed.

Keyword Index

Carbon flux, water flux, mosses, arctic ecosystems

Introduction

Arctic systems play an important role in the global carbon cycle (Oechel *et al.* 1993; Oechel *et al.* 2000). Global warming is expected to have a large impact on both soil respiration and primary production of arctic plants, thereby potentially changing the Arctic from a net sink to a source of carbon ((Oechel *et al.* 1993; Oechel *et al.* 2000; Shaver *et al.* 1992). Insight into processes driving carbon fluxes is thus essential to predict changes in the carbon stocks in arctic ecosystems. Recent research has focused on measuring and predicting regional carbon budgets (Lloyd 2001, see Baldocchi 2003 for an overview). As arctic ecosystems are characterized by a heterogeneous mix of vegetation types over short distances (Shaver & Chapin 1991; van Wijk & Williams 2005), often in relation to topography (Walker & Everett 1991), it is necessary to study the effects of this diversity of vegetation types on regional carbon fluxes to increase the reliability of these regional estimates. Williams *et al.* (2006) studied carbon exchange of different vegetation types in detail along a toposequence in Northern Alaska, and concluded that more detail is needed to prevent mismatch between fine scale variation and larger scale estimates using eddy flux towers. Although much is known already about fine scale variation in vascular plant processes, less information is available about the importance of mosses in these systems.

Shaver & Chapin (1991) showed that mosses are important members of arctic plant communities, representing up to 50% of the total aboveground biomass in wet sites near Toolik Lake. Moss biomass is not constant, but is highly responsive to global change treatments, for example it is affected by increased nutrient inputs by acidic deposition and enhanced nutrient availability by soil warming. Mosses in sub arctic and high arctic systems responded differently to these treatments. In the sub arctic enhanced nutrient input lead to a decrease in moss biomass (van Wijk *et al.* 2004; Potter *et al.* 1995; Chapin & Shaver 1985) while in the high Arctic moss biomass increased, especially in open vegetation (Robinson *et*

al. 1998; Gordon *et al.* 2001). Wasley *et al.* (2006) also found positive responses of mosses to nutrient additions in Antarctic systems.

Mosses play an important role in the functioning of arctic ecosystems. They act as a selective layer for nutrient leaching and an insulative layer with respect to heat transport from soil to atmosphere and vice versa (Beringer *et al.* 2001; Oechel & van Cleve 1986; Skre & Oechel 1981). Mosses have been shown to be important in the carbon and water exchange of ecosystems with high moss biomass in the high Arctic, and in spring and autumn in low as well as the high Arctic when plant leaves are not fully developed (Hicklenton & Oechel 1976). However, mosses are not well represented in thermo-dynamic arctic models (Beringer *et al.* 2001). Models predicting evaporative losses in arctic systems generally tend to overestimate water losses, partly because moss dynamics are not included (McFadden, Eugster & Chapin 2003; Lynch *et al.* 1999). In the past some site specific studies in the arctic tundra were performed (Sommerkorn, Bolter & Kappen 1999; Hicklenton & Oechel 1976) in which the change in moss contribution to ecosystem carbon exchange was quantified over the seasons. However, until now no general relationships were found to predict carbon and water fluxes of mosses across sites.

Our study aimed to quantify the contribution of mosses to the carbon and water exchange of a range of arctic vegetation types with high moss cover in Northern Sweden and on Svalbard. Furthermore, this study attempts to relate this contribution to ecosystem properties such as leaf area index and spectral reflectance (e.g. the normalized difference vegetation index, NDVI (Rouse *et al.* 1974)) across different moss species, the two landscapes at different latitudes, and multiple vegetation types and climatic conditions. NDVI is calculated from the visible and near-infrared light reflected by vegetation. Green vegetation absorbs most of the visible light that hits it, and reflects a large portion of the near-infrared light, whereas sparse vegetation reflects more visible light and less near-

infrared light. NDVI can therefore be used to estimate the greenness of vegetation, or the leaf area index of vegetation, and can be measured easily across a range of scales using hand held equipment or satellite images. NDVI has been related to the carbon exchange of arctic vegetation (Boelman *et al.* 2003). Our hypothesis is that the contribution of mosses to the water and carbon exchange across a wide range of moss species, vegetation types and growing conditions can be related to system characteristics that can be measured relatively easily (e.g. Van Wijk & Williams 2005), thereby assuring a broad applicability of the relationships.

Materials and Methods

Study area

Measurements were made at two locations within the Arctic, around Abisko (Sweden, 68°21'N, 18°49'E) and around Longyearbyen (Svalbard, 78°21'N, 15°70'E). The sites at Svalbard (annual precipitation 200 mm, average annual July temperature 5 °C) were selected so as to include a representative range of vegetation types. In the Abisko area (annual precipitation 225-475 mm, average July temperature 12 °C) two sites were selected. One site is located close to the Abisko Scientific Research Station above the tree line (altitude 540 m above sea level) and is characterized by a distinct heterogeneity in vegetation types over a relatively a small area (van Wijk & Williams 2005). The other site is located in a mire (Stordalen 68°35'N, 19°04'E) and the plots in this site are dominated by *Eriophorum* and *Carex* species and *Sphagnum*.

Within each area a range of plots were selected representing the most important vegetation types based on the circum-arctic classification used by Walker *et al.* (2005) and for the Abisko region also based on Van Wijk, Williams & Shaver (2005). By covering the key vegetation types in the two locations we make sure that any relationship we find has a broad applicability and that the sampling scheme is not biased. As the focus of this study was on moss primary production we performed the measurements in plots with a high moss cover (100% or near 100%) but with a wide range of vascular plant cover. Table 1 shows the important vegetation types with the dominant plants and moss species. A wide range of moss species was sampled within this study to test whether generally applicable relationships could be found between vegetation and site characteristics and the moss contribution to carbon and water exchange across these moss species. Flux measurements were performed at the end of June and mid August in the Abisko area and in July and early August in the Longyearbyen area. In total 876 CO₂ and 899 H₂O chamber measurements were collected at

17 plots in Abisko and 21 plots at Svalbard.

Experimental setup

CO₂ and H₂O fluxes were measured using an acrylic plastic chamber (0.30 x 0.30 x 0.19m). After selecting a site an iron frame with legs was put into the soil. A transparent plastic skirt hung from the frame to the ground surface, with a heavy steel chain used to seal the plastic to the ground around the perimeter of the frame (Williams *et al.*, 2006; Street *et al.* 2007). H₂O and CO₂ concentration changes were measured for a period of 30 seconds with a gas analyzer (Li-Cor 6400, Li-Cor Inc. Lincoln, Nebraska, USA) which was connected to the chamber. The chamber and the gas analyzer were run in a closed system set up, and mixing of the air within the chamber was done with a fan. Testing in the lab revealed no leaks over the short measurement periods that were used in our methodology, in which, because of these short measurement periods, only relatively small CO₂ gradients developed between the air inside and outside of the chamber. The short time frame over which measurements were taken also assured that adsorption of CO₂ and H₂O was not influencing our results (Bloom *et al.* 1980; Hari *et al.* 1999). In addition the photosynthetic photon flux density (*PPFD*), the air temperature and the temperature of the mosses were recorded by the gas-analyzer using its standard *PPFD* sensor and thermocouples.

To test the effect of the light flux on CO₂ and water fluxes, light intensity was changed artificially. Usually two measurements were done under ambient light, followed by three levels of shading, followed by three dark measurements. Shading was done by placing one, two, or three thicknesses of plastic window screen material over the top and sides of the chamber. Dark respiration was estimated by putting a dark cover (tarpaulin) over the chamber and reducing light intensity in this way to zero. Respiration of the plot was determined by averaging the three dark measurements. Following the approaches of

Williams *et al.* (2006), Street *et al.* (2007) and Shaver *et al.* (2007), measurements were taken at different moments during the day to cover diurnal variations in air temperature. Detailed analyses of the data of these studies showed no effects of time of day (which could be a proxy for the carbo-hydrate status of the plants) on the measured carbon fluxes.

To determine the contribution of mosses to the gas exchange of the plot, first, the light response of the whole plot was measured (plants, mosses and soil). After completing a light response series, all vascular plants were removed by cutting stems and leaves as low as possible without damaging the moss layer, and making sure that all green leaves of the vascular plants were removed. This meant in practice that in general plants were cut at the moss surface level. The frame was not removed during the harvest to avoid the effect of CO₂ discharge out of the soil. A second light response curve was collected immediately after removing the vascular plants. Because of enhanced wound respiration of the vascular plants, which could possible form a substantial part of the small carbon fluxes of the moss system, we did not use these measurements for determining net ecosystem carbon exchange of the mosses. However, gross primary production (GPP) of the mosses can be calculated by subtracting the dark respiration from the measurements made at each light level.

The temperature in the moss layer, and at 5 and 10 cm depth in the soil, together with the soil moisture content (Hydrosense Water Content Sensor with 20 cm tines, Campbell Scientific) were recorded as soil respiration is strongly affected by these two soil characteristics.

After measuring CO₂ and H₂O fluxes of the total system as well as of the mosses separately, the moss layer was harvested, stored in a sealed plastic bag, transported to the lab where the species composition and the water content of the mosses was determined. The water content was calculated using the ratio of (fresh weight– dry weight)/dry weight. The thickness of the photosynthetically active moss layer was estimated by measuring the green

part of the mosses. The total leaf area of the vascular plants in the plots and the leaf area per vascular plant species were determined after harvest using a scanner and software package (Canon Canoscan LiDE 30 colour image scanner in conjunction with Winfolia software, Regent Instruments Inc.).

A small, unreplicated, watering experiment was performed on Svalbard to test the effect of water on thickness of the green moss active layer, moss water content, GPP and NDVI of *Racomitrium panschii* (no cf.) species dominated plot. These characteristics were measured both before and after watering.

Both before and after harvest of the vascular plants we used a scanning spectroradiometer (Unispec, PP Systems, Amesbury, Massachusetts, USA) to determine the normalized difference vegetation index (NDVI; Boelman *et al.* (2003)). NDVI was calculated by the formula:

$$NDVI = (R_{IR} - R_{VIS}) / (R_{IR} + R_{VIS}) \quad (1)$$

where: R_{IR} = reflectance at 725-1000 nm, and R_{VIS} =reflectance at 570-680 nm (Rouse *et al.* 1974).

From the water and carbon dioxide concentrations recorded by the gas analyzer the carbon dioxide and water fluxes were calculated, similar to Williams *et al.* (2006). This was done with the two formulas:

$$F_c = \frac{\rho V \frac{dC}{dt}}{A} \quad (2a)$$

in which F_c is the net carbon dioxide flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$), ρ is the air density (mol m^{-3}), $\frac{dC}{dt}$ is the change of the CO_2 concentration over time ($\mu\text{mol mol}^{-1} \text{s}^{-1}$), A is the surface area of the measured plot (m^2) and V is the volume of the chamber and frame (m^3). To get an accurate volume estimation of the chamber, 9 depth measurements from the top of the chamber base

to the soil surface were done. The volume of the chamber (0.0161 m^3) is added to this volume. The same formula as for CO_2 can be applied for calculating the water flux, in which F_w is the net water flux ($\text{mmol.m}^{-2}.\text{s}^{-1}$) and $\frac{dW}{dt}$ is the changing water concentration over time ($\text{mmol mol}^{-1} \text{ s}^{-1}$).

$$F_w = \frac{\rho V \frac{dW}{dt}}{A} \quad (2b)$$

We assumed that our dark measurements of F_c were equivalent to system respiration (R_e) and calculated system GPP (gross primary productivity) as $R_e - F_c$. Similar to this, gross water loss (GW) was calculated as F_w minus the dark evaporation of mosses and soil (E_{dark}).

Data Analysis

To compare differences in CO_2 and H_2O fluxes between moss and plant species, and relate these differences to the environmental conditions a simple model was used to describe gas exchange responses of the vegetation:

$$GPP = \frac{P_{MAX} PPFD}{k + PPFD} \quad (3)$$

In which P_{max} is the maximum CO_2 flux at saturating $PPFD$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), $PPFD$ is the incoming photosynthetic photon flux density ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), k is a half saturation constant of photosynthesis ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). A nonlinear optimization solver was used to fit the data. K was forced to be $\leq 400 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ to ensure a saturating light-response curve within an acceptable $PPFD$ range. As sometimes the solver had difficulty finding a reliable P_{max} value, we also quantified saturated GPP based directly on data using the measured CO_2 flux in the saturating part of the light response curve ($PPFD > 600 \mu\text{mol m}^{-2} \text{ s}^{-1}$). This variable we will denote as GPP_{max} . Measurements across the different sites showed

saturation of GPP at these values of PPFD, although the modelled response using Equation 3 was not always able to capture that saturation properly (e.g., see Figure 1a). The initial light use efficiency (LUE) is calculated by dividing GPP by the PPFD value for measurements with $PPFD \leq 200 \mu\text{mol m}^{-2} \text{s}^{-1}$. This trajectory was used, because in this trajectory the response of GPP to PPFD was close to linear and enough measurements could be collected in the field for a reliable estimate.

To calculate the actual contribution of the mosses to the overall ecosystem GPP and water exchange we had to correct for light extinction by the canopy layer in the moss GPP response curve (as we removed the vascular plant canopy while estimating moss gas exchange). For this purpose the model of Lambert Beer was used:

$$PPFD = PPFD_{ambient} e^{-rLAI} \quad (5)$$

The extinction coefficient (r) was set at 0.5, equal to Herbert *et al.* (1999), who simulated light extinction in similar arctic vegetation. As the variation in the extinction coefficients of the dominant vascular plants is high, the sensitivity of the model outcome to changes in r (plus or minus 20%) was checked. The corrected $PPFD$ was entered in the GPP moss model and a new GPP was calculated. The same was done for the water-model. In this correction approach we assume a homogeneous distribution of the canopy over the plot.

The response of ecosystem level water exchange to $PPFD$ was simulated with a simple model assuming a linear relationship between $PPFD$ and the evaporation of the whole system minus the dark evaporation:

$$E_{total} = c_{total} * PPFD \quad (6)$$

Where E_{total} is the evapotranspiration of the total system in $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$. After harvesting of the vascular plants, the response of evaporation of mosses and the soil to $PPFD$ was quantified, also assuming a linear response, after subtracting the evaporation estimated during the three dark measurements:

$$E_{\text{mosses}} = c_{\text{mosses}} * \text{PPFD} \quad (7)$$

Where E_{mosses} is the evaporation of the mosses in $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$.

The Lambert Beer law was used to estimate the reduced light intensities in the understorey and to calculate in this way the actual contribution of the mosses to water losses. As there is a non-linear relationship between PPFD intercepted by the vascular plant canopy and vascular plant LAI, this means that a new coefficient had to be calculated between moss evaporation and PPFD ($c_{\text{mosses_corrected}}$):

$$E_{\text{mosses}} = c_{\text{mosses_corrected}} * \text{PPFD} \quad (8)$$

Next the water exchange of the mosses was subtracted from the measurements of the whole system and a model was fitted through the remaining flux:

$$\text{Transp} = c_{\text{vascular}} * \text{PPFD} - d \quad (9)$$

Where Transp is transpiration by the vascular plants in $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. Parameter d is used to set the remaining flux at zero PPFD at zero. The contribution of the mosses to the system responsiveness to PPFD was calculated by dividing E_{mosses} , calculated using equation 8, by E_{total} .

A statistical analysis was performed using (multiple) regression techniques for investigating empirical relationships. Relations were considered significant at $P < 0.05$.

Results

Carbon exchange

The vegetation types sampled in this study showed a broad range of values of the leaf area index (LAI) of the vascular plants: the LAI of the plots in Abisko ranged from 0.04 to 1.37 m² leaf/m² ground area, and in Longyearbyen from 0 to 0.49 m² leaf/m² ground area.

Twenty-five complete light curves (i.e., those including saturating or almost saturating GPP) were collected in sites where both vascular plants and mosses were present. The performance of the system level GPP response model (Eqn. 3) was good (the average of all the individual curve fit R^2 values was 0.90 ± 0.11 SD). An example is given of the light response curve of a *Betula* and *Hylocomium* dominated plot (Figure 1a). After harvesting the plants a new light curve was estimated. To calculate the actual contribution of the mosses, the light-curve of the mosses was corrected for light extinction by leaves. This corrected light curve is also shown in Figure 1a. Analysis of the extinction coefficient r showed a low sensitivity of the calculated GPP to changes in r . A 20% change in r led to a 2% ($\pm 2\%$) change in GPP. For each plot the P_{\max} and the half-saturation constant (k) of the plants and mosses were calculated. The contribution of the mosses is calculated by dividing P_{\max} of the mosses by P_{\max} of the total system. The contribution of the mosses varied from almost 100% at sites with a low LAI to 20% at sites with a high LAI, and showed a significant negative relation with LAI (Figure 1b).

P_{\max} of the whole system was positively related with the LAI of the system (Figure 1c). However, LAI was a better predictor for the P_{\max} of vascular plants only ($R^2=0.58$) compared to the whole system ($R^2=0.18$) (Figure 1c). The light response model was used to obtain the corrected moss fluxes and the P_{\max} values of the whole system.

GPP_{\max} of mosses showed a significant exponential relationship with NDVI (Figure 2a, $R^2=0.65$). Combining the GPP_{\max} and NDVI values of the total system and of mosses

only showed that these data points fall in more or less the same relationship. In Figure 2b NDVI is plotted against the measured initial light use efficiency (LUE, $\mu\text{mol CO}_2/\mu\text{mol photons}$) of the mosses and of the whole system. Except for one obvious outlier a similar exponential relationship as for NDVI and GPP_{max} can be drawn for the initial light use efficiency and NDVI ($R^2=0.57$).

Dark respiration of the whole system is strongly related to soil temperature and showed the best relationship with soil temperature at 5 cm depth (Figure 3). Moss respiration is not shown in this figure because of enhanced wound respiration of the plants.

Surprisingly, moss temperature showed no strong relationships with the photosynthetic characteristics GPP_{max} and the initial LUE (results not shown).

Water exchange

Figure 4a shows the performance of the linear response model of water exchange and *PPFD* for the whole system, for mosses only and for light extinction corrected moss response curve. The overall performance of the linear response model of the water exchange was lower than the carbon flux response model: here the average R^2 was 0.77 (and a standard deviation of the R^2 values of 0.15). The effect of LAI on the contribution of mosses to the overall water exchange response to *PPFD* is shown in Figure 4b: The contribution varied between 140% and 20%. The value of circa 140% was a clear example of the relatively large uncertainty in the water flux data and the poorer performance of the linear water response model as compared with the carbon response model: theoretically this value cannot exceed 100% as we are dealing with relative measures.

Basal system evaporation (evaporation measured in the dark) was strongly related to moss temperature (Figure 5a). In one plot basal system evaporation was negative, which means a decrease in the water concentration of the air during the measurement cycle. This

indicates either a measurement error or absorption of water vapour by the relatively dry mosses (these mosses had a relatively small water content of 17%). The evaporation coefficient of the mosses (see Equation 5) was positively related to the water content of the mosses: the higher the water content of the mosses, the steeper the slope of evaporation response (Figure 5b). The response coefficient of vascular plant transpiration (Equation 9, c_{vascular}) showed a clear relationship with LAI, whereas the whole system coefficient (Equation 6, c_{total}) did not (Figure 5c).

When water was added in the small experiment (Table 2), the thickness of the “active” upper green layer of moss, water content and NDVI all increased considerably and the GPP increased eight fold within an hour after watering.

NDVI increased asymptotically with the thickness of the green moss layer (Figure 6; R^2 0.48). This thickness of the green layer is related in part to moss water content (R^2 of 0.5, results not shown) indicating that an increase in water content leads to an increase in the active layer thickness, although these variables are not independent.

Discussion

Our results demonstrated that photosynthetic characteristics of mosses and moss contribution to carbon and water fluxes at the ecosystem level can be related to ecosystem characteristics such as NDVI and the LAI of vascular plants that are relatively easy to measure remotely. As the Arctic is characterized by a large spatial heterogeneity (Bliss, Heal & Moore 1981; Shaver *et al.* 1996) such relationships are important to understand and quantify if we want to predict the carbon and water exchange of arctic vegetation types across the landscape. Although our study concentrated on vegetation types with high moss cover (close to 100%), it shows the potential for deriving such simple relationships between ecosystem characteristics and the complex dynamic processes in these ecosystems. The number of sites for which light curves were collected was relatively limited (i.e. 25), but we did cover a wide range of growing conditions and moss species (see Table 1). Further research on other arctic sites will show whether the relationships found in this study can also be applied outside of the growing conditions of Abisko and Svalbard and the moss and plant species found in these locations. In our sites the moss contribution to the photosynthetic capacity of the ecosystem varies from almost 96% in plots with low LAI to 14% in plots with a high vascular plant cover (Figure 1b) and shows a strong negative correlation with LAI. Several studies have focused on moss contribution to photosynthesis in forests (Heijmans, Arp & Chapin 2004; Drewitt *et al.* 2002; Goulden *et al.* 1998) showing a contribution varying from negligible (Drewitt *et al.* 2002) to 10 to 50% (Goulden & Crill 1997). The relative contribution of mosses to system level carbon exchange in the Arctic can thus be substantially greater than in forest systems. Although other studies previously quantified the contribution of mosses to arctic ecosystem level carbon exchange over time (Oechel & Collins 1976; Sommerkorn *et al.* 1999), these studies were site specific, and no general relationships across the landscape were derived. It is important to realize here that the

relationship between moss contribution to system level GPP and LAI (Fig. 1b) is derived for plots with high moss cover. We expect it to become less clear if also plots with lower moss cover are also included. Figure 1b therefore represents the upper border of moss contribution to system level GPP.

The decrease in contribution of mosses with increasing vascular plant LAI can be explained by two underlying processes. First, an increasing canopy density (vascular plant LAI) leads to a decrease in the amount of light that reaches the moss layer, thereby resulting in a decrease in GPP of the mosses. And second, the contribution of vascular plants increases because their photosynthetic capacity increases with increasing leaf area (Figure 1c). An increase in LAI leads to an increase in both the P_{\max} of the total system and of the vascular plants. Furthermore, the slope of the regression line between P_{\max} and LAI at the ecosystem level was smaller than at vascular plant level, showing the decreasing relative contribution of mosses to system level P_{\max} with increasing LAI. From our results it is clear that in moss dominated systems LAI is not a good predictor for ecosystem level GPP (Figure 1c).

Williams *et al.* (2006) also found a relationship between P_{\max} and LAI in their study in Northern Alaska, but with a relatively large uncertainty which they attributed to the error in the LAI estimates. However based on our results, it seems more likely that the GPP – LAI uncertainty is caused at least in part by the presence of mosses in these systems.

NDVI is a good predictor of CO₂ exchange characteristics of mosses (Figure 2a and b). A strong correlation is found between NDVI and GPP_{\max} of mosses across different moss species, two latitudes, vegetation types and climatic conditions. Whiting (1994) observed problems in relating the NDVI of *Sphagnum* spp to carbon exchange characteristics and suggested the development of new relationships between carbon exchange of mosses and remote sensing techniques. Our study, however, shows that across moss species, NDVI is a good predictor of both the initial light use efficiency (LUE) and the photosynthetic capacity.

Furthermore, the relationship between the GPP_{max} of moss systems and NDVI seems to fit in well with the overall relationship between GPP_{max} and NDVI of systems with vascular plants (Figure 2a and b). Further research is needed to test whether the relationships between NDVI and the photosynthetic parameters also hold for plots with moss cover less than 100%. The respiration coefficient of the vegetation types measured in this study shows a strong relation with soil temperature (Figure 3a). However, temperature showed no clear effect on moss photosynthetic characteristics (Figure 3b and c). Apparently the effects of growing condition and moss species on these characteristics are overruling any effects that temperature has. Also a part of the possible temperature effect is captured in the PPFD relationships in our analysis, as these factors are correlated.

The relationships of NDVI with the photosynthetic characteristics of mosses can be interpreted as having a functional significance, because NDVI also showed correlations with moss characteristics such as active layer depth (Figure 6). For vascular plants NDVI is a good measure of the solar radiation absorbance capacity of the canopy and can be related to leaf area of vascular plants (Tucker, 1979; Boelman *et al.* 2003). The leaf area of moss is hard to determine and therefore the thickness of the active green layer of mosses was used as an indicator.

In the water addition experiment GPP increased more than 8 fold and also the active layer thickness increased substantially (Table 2). Although no robust conclusions can be drawn based on this small experiment, the results support the idea that thickness of the active layer is related to moss water content and that with increasing thickness of the active layer GPP of mosses increases as well. Furthermore, NDVI shows a clear increase after watering the mosses. This change in NDVI is in correspondence with Vogelmann & Moss (1993) who observed changes in reflectance with changing water content in *Sphagnum* species. The results are in contrast to the study of Lovelock & Robinson (2002) in which a strong

relationship between total chlorophyll concentration of mosses and NDVI was found, but no relationship between NDVI and water content.

Mosses are not only important with respect to carbon exchange, but they clearly also play an important role in the water exchange of Arctic ecosystems (Figure 4b). Although the relationship is much less clear than in the analysis of the carbon exchange, LAI shows a significant relationship with the moss contribution to system level water exchange. LAI is related linearly to the transpiration of vascular plants, but it shows no relationship at all to the water exchange of the whole system. This result is similar to the one obtained for the carbon exchange, although in that case LAI still shows a significant correlation with system level P_{\max} , whereas for water no relationship existed. As expected, the evaporative loss of mosses per incoming photon is related to moss water content (Figure 5b). The basal system evaporation of moss plots plot was strongly related to moss temperature (Figure 5a), which is expected from an energy balance point of view. Vascular plants do not contribute to this basal system evaporation; it is only the sum of soil and moss evaporation.

The results of the water exchange data are less easy to interpret than those of the carbon exchange. This is mainly due to a build-up of errors and the lower performance of the water exchange – irradiance response model, explaining the wide range of relative contributions at an LAI value of zero m^2 leaf per m^2 surface area (Figure 5c), where one would expect a vascular plant contribution of zero to system evaporation. Because of discrepancies between model and measurement this is often not the case. In contrast to the modelling error of the light-response curve of the carbon dioxide model, which is fitted with two parameters, each characterizing a separate part of the light response curve, the coefficient of the linear water response is more sensitive to deviations of individual measurement points.

In this study the carbon and water exchange of moss dominated systems is quantified

and related to system properties. LAI and NDVI are reasonable predictors of carbon and water exchange of mosses in sites with high moss cover. In this study the moss contribution varied along large latitudinal and topographic gradients and we did not quantify the temporal development of moss gas exchange throughout the year. Oechel & Collins (1976) and Sommerkorn *et al.* (1999) performed site specific studies in the arctic tundra and they were able to quantify the change in moss contribution within and between seasons. Mosses are important at sites with low vascular plant density as well as in the shoulder (spring and autumn) seasons, especially in spring when the vascular canopy is not fully developed and when mosses are less subject to drought because of recent snowmelt. Furthermore, experiments in the past showed a well-developed capacity of mosses to acclimate to their environment. Positive assimilation rates of mosses have been measured below 0°C (Valanne 1985). Also freezing is not a hazard. In *Racomitrium lanuginosum*, an arctic moss species, reactivation occurs within a few hours, even after temperatures of -30°C (Valanne 1985). This supports the suggestions that the higher carbon and water exchange contribution of mosses are larger during spring and autumn.

To better understand the dynamic development of the moss contribution to ecosystem carbon and water exchange over the seasons, more insight is needed on the controls over moss physiology and the phenological development of both mosses and vascular plants. To track leaf area development during the growing season a less rigorous LAI-method than harvesting must be chosen and a better predictor for the photosynthesizing area of mosses should be developed. Leaf area as a measure of photosynthesizing area cannot easily be applied to mosses. As not only moss cover is an important determinant of GPP, but also the thickness of the green layer, this means that using green moss volume as a predictor for photosynthesizing area would probably improve the prediction of GPP. As we selected our plots for 100% moss cover, we are not able to show the effect of moss cover and density on

their contribution to ecosystem level fluxes.

From this study a relatively complex relationship arises between LAI, moss cover and moss contribution to carbon and water exchange. Increasing moss cover leads to an increase in the moss contribution to system level carbon and water exchange, whereas increasing vascular plant LAI leads to a decrease. However, we expect moss cover and LAI not to be totally independent variables and we expect the relationship between LAI and moss cover to be complex, with a lot of scatter caused by environmental conditions. Even in coniferous forests with, compared to arctic systems, high LAI values, moss covers of close to 100% can occur. Furthermore, if one aims at the dynamic prediction of moss photosynthesis a quantification of the influence of water dynamics on carbon and water exchange of mosses is needed (Lloyd, 2001).

Acknowledgements

We acknowledge funding from the US National Science Foundation to the Marine Biological Laboratory (NSF Grant # OPP-0352897). We thank B. Kaye, L.E. Street and C. Ronfort for their great help and support during fieldwork, J.H.C. Cornelissen for his help with determining mosses, and K.E. Giller, subject editor Steve Long and two anonymous referees for their comments on the manuscript.

References

- Baldocchi D.D. (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, **9**, 479-492.
- Beringer J., Lynch A.H., Chapin F.S., Mack M. & Bonan G.B. (2001) The representation of arctic soils in the land surface model: The importance of mosses. *Journal of Climate*, **14**, 3324-3335.
- Bliss L.C., Heal O.W. & Moore J.J. (1981) *Tundra ecosystems: a comparative analysis*. Cambridge University Press, Cambridge.
- Bloom A.J., Mooney H.A., Bjorkman O. & Berry J. (1980) Materials and methods for carbon dioxide and water exchange analysis. *Plant, Cell and Environment*, **3**, 371 - 376.
- Boelman N.T., Stieglitz M., Rueth H., Sommerkorn M., Griffin K.L., Shaver G.R. & Gamon J.A. (2003) Response of NDVI, Biomass, and Ecosystem Gas Exchange to Long-Term Warming and Fertilization in Wet Sedge Tundra. *Oecologia*, **135**, 414 - 421.
- Chapin F.S. & Shaver G.R. (1985) Individualistic Growth-Response of Tundra Plant-Species to Environmental Manipulations in the Field. *Ecology*, **66**, 564-576.
- Drewitt G.B., Black T.A., Nesic Z., Humphreys E.R., Jork E.M., Swanson R., Ethier G.J., Griffis T. & Morgenstern K. (2002) Measuring forest floor CO₂ fluxes in a Douglas-fir forest. *Agricultural and Forest Meteorology*, **110**, 299-317.
- Gordon C., Wynn J.M. & Woodin S.J. (2001) Impacts of increased nitrogen supply on high Arctic heath: the importance of bryophytes and phosphorus availability. *New Phytologist*, **149**, 461-471.
- Goulden M.L. & Crill P.M. (1997) Automated measurements of CO₂ exchange at the moss surface of a black spruce forest. *Tree Physiology*, **17**, 537-542.

- Goulden M.L., Wofsy S.C., Harden J.W., Trumbore S.E., Crill P.M., Gower S.T., Fries T., Daube B.C., Fan S.M., Sutton D.J., Bazzaz A. & Munger J.W. (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214-217.
- Hari P., Keronen P., Back J., Altimir N., Linkosalo T., Pohja T., LKulmala M. & Vesala T. (1999) An improvement of the method for calibrating measurements of photosynthetic CO₂ flux. *Plant, Cell and Environment*, **22**, 1297 - 1301.
- Heijmans M., Arp W.T. & Chapin F.S. (2004) Carbon dioxide and water vapour exchange from understory species in boreal forest. *Agricultural and Forest Meteorology*, **123**, 135-147.
- Herbert D.A., Rastetter E.B., Shaver G.R. & Agren G.I. (1999) Effects of plant growth characteristics on biogeochemistry and community composition in a changing climate. *Ecosystems*, **2**, 367-382.
- Hicklenton P.R. & Oechel W.C. (1976) Physiological Aspects of Ecology of *Dicranum-Fuscescens* in Subarctic .1. Acclimation and Acclimation Potential of Co-2 Exchange in Relation to Habitat, Light, and Temperature. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **54**, 1104-1119.
- Lloyd C.R. (2001) The measurement and modelling of the carbon dioxide exchange at a high Arctic site in Svalbard. *Global Change Biology*, **7**, 405-426.
- Lovelock C.E. & Robinson S.A. (2002) Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. *Plant Cell and Environment*, **25**, 1239-1250.
- Lynch A.H., Chapin F.S., Hinzman L.D., Wu W., Lilly E., Vourlitis G. & Kim E. (1999) Surface energy balance on the arctic tundra: Measurements and models. *Journal of Climate*, **12**, 2585-2606.
- McFadden J.P., Eugster W. & Chapin F.S. (2003) A regional study of the controls on water

- vapor and CO₂ exchange in arctic tundra. *Ecology*, **84**, 2762-2776.
- Oechel W.C. & Collins N.J. (1976) Comparative Co₂ Exchange Patterns in Mosses from 2 Tundra Habitats at Barrow, Alaska. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **54**, 1355-1369.
- Oechel W.C., Hastings S.J., Vourlitis G., Jenkins M., Riechers G. & Grulke N. (1993) Recent Change of Arctic Tundra Ecosystems from a Net Carbon-Dioxide Sink to a Source. *Nature*, **361**, 520-523.
- Oechel W.C. & van Cleve K. (1986) The role of Bryophytes in Nutrient Cycling in the Taiga. In: *Forest Ecosystems in the Alaskan Taiga, Ecological Studies 57* (eds K. van Cleve, F.S. Chapin, P.W. Flanagan, L.A. Viereck, & C.T. Dyrness), pp. 121-137. Springer Verlag, New York.
- Oechel W.C., Vourlitis G.L., Hastings S.J., Zulueta R.C., Hinzman L. & Kane D. (2000) Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978-981.
- Potter J.A., Press M.C., Callaghan T.V. & Lee J.A. (1995) Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. *New Phytologist*, **131**, 533-541.
- Robinson C.H., Wookey P.A., Lee J.A., Callaghan T.V. & Press M.C. (1998) Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology*, **79**, 856-866.
- Rouse J.W., Haas R.H., Schell J.A., Deering D.W. (1974) Monitoring vegetation systems in the great plains with ERTS. In: *Proceedings of the 3rd earth resources technology satellite-1 symposium, Greenbelt: NASA SP-351*, pp 301 - 317.
- Shaver G.R., Billings W.D., Chapin F.S., Giblin A.E., Nadelhoffer K.J., Oechel W.C. & Rastetter E.B. (1992) Global Change and the Carbon Balance of Arctic Ecosystems.

- Bioscience*, **42**, 433-441.
- Shaver G.R. & Chapin F.S. (1991) Production - Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, **61**, 1-31.
- Shaver G.R., Laundre J.A., Giblin A.E. & Nadelhoffer K.J. (1996) Changes in live plant biomass, primary production and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research*, **28**, 363-379.
- Shaver G.R., Street L.E., Van Wijk M.T. & Williams M. (2007). Functional convergence in regulation of net CO₂ flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, **in press**.
- Skre O. & Oechel W.C. (1981) Moss Functioning in Different Taiga Ecosystems in Interior Alaska .1. Seasonal, Phenotypic, and Drought Effects on Photosynthesis and Response Patterns. *Oecologia*, **48**, 50-59.
- Sommerkorn M., Bolter M. & Kappen L. (1999) Carbon dioxide fluxes of soils and mosses in wet tundra of Taimyr Peninsula, Siberia: controlling factors and contribution to net system fluxes. *Polar Research*, **18**, 253-260.
- Street L.E., Shaver G.R., Williams M., Van Wijk M.T. (2007) What is the relationship between changes in canopy leaf area and changes in photosynthetic CO₂ flux in arctic ecosystems? *Journal of Ecology*, **95**, 139-150.
- Tucker C.J. (1979) Red and Photographic Infrared Linear Combinations for Monitoring Vegetation. *Remote Sensing of Environment*, **8**, 127-150.
- Valanne N. (1985) Photosynthesis and photosynthetic products in mosses. In: *The experimental Biology of Bryophytes* (eds A.F. Dyer & J.G. Duckett), pp. 257-273. Academic Press, London.
- van Wijk M.T., Clemmensen K.E., Shaver G.R., Williams M., Callaghan T.V., Chapin F.S., Cornelissen J.H.C., Gough L., Hobbie S.E., Jonasson S., Lee J.A., Michelsen A.,

- Press M.C., Richardson S.J. & Rueth H. (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.
- van Wijk M.T. & Williams M. (2005) Optical instruments for measuring leaf area index in low vegetation: Application in Arctic ecosystems. *Ecological Applications*, **15**, 1462-1470.
- Van Wijk M.T., Williams M. & Shaver G.R. (2005) Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, **142**, 421 - 427.
- Vogelmann J.E. & Moss D.M. (1993) Spectral Reflectance Measurements in the Genus *Sphagnum*. *Remote Sensing of Environment*, **45**, 273-279.
- Walker D.A. & Everett K.R. (1991) Loess Ecosystems of Northern Alaska - Regional Gradient and Toposequence at Prudhoe Bay. *Ecological Monographs*, **61**, 437-464.
- Walker D.A., Raynolds M.K., Daniels F.J.A., Einarsson E., Elvebakk A., Gould W.A., Katenin A.E., Kholod S.S., Markon C.J., Melnikov E.S., Moskalenko N.G., Talbot S.S. & Yurtsev B.A. (2005) The circumpolar Arctic vegetation map. *Journal of Vegetation Science*, **16**, 267 - 282.
- Wasley J., Robinson S.A., Lovelock C.E. & Popp M. (2006) Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Global Change Biology*, **12**, 1800 - 1812.
- Whiting G.J. (1994) CO₂ Exchange in the Hudson-Bay Lowlands - Community Characteristics and Multispectral Reflectance Properties. *Journal of Geophysical Research-Atmospheres*, **99**, 1519-1528.
- Williams M., Street L.E., van Wijk M.T. & Shaver G.R. (2006) Identifying differences in carbon exchange among arctic ecosystem types. *Ecosystems*, **9**, 288-304.

Table 1 Location and the most important plant- and moss species of the measured sites (for Stepps site, see <http://www.dur.ac.uk/stepps.project/>)

Location		Vegetation Type (moisture)	Number of plots	Dominating plant species	Dominating moss and liverworth species
Abisko	Stepps	Wet Sedge (wet)	5	<i>Sedge (Carex spp, Eriophorum) , Graminoids</i>	<i>Sphagnum fuscum, Sphagnum spp.</i>
		Betula (medium)	4	<i>Betula nana, Empetrum nigrum, Vaccinium uliginosum, Andromeda polifolia</i>	<i>Hylocomium splendens, Ptilidium ciliare, Dicranum spp, Tomentypnum nitens, Amblystegiaceae, Ptilium crista-castrensis.</i>
		Heath (dry)	4	<i>Empetrum nigrum, Vaccinium uliginosum, Rhododendron laponicum, Andromeda polifolia,</i>	<i>Aulacomnium turgidum, Dicranum spp, Rhytidium rugosum</i>
	Stordalen	Peat Bog (wet)	4	<i>Sedge (Carex, Eriophorum)</i>	<i>Sphagnum spp.</i>
Longyear-byen		Productive Graminoids (wet)	5	<i>Carex, Eriophorum, Graminoids</i>	<i>Calliergon sarmentosum, Calliergon richardsonii, Sphagnum spp, Aulacomnium spp, Bryum cryophilum</i>
		Salix (wet)	5	<i>Salix polaris, Graminoids</i>	<i>Pohlia obtusifolia, Polytrichum spp, Calliergon stramineum, Aulacomnium turgidum</i>
		Heath (dry)	5	<i>Equisetum spp, Betula nana, Salix polaris</i>	<i>Drepanocladus cossonii, Tomentypnum nitens, Sanionia uncinata, Aulacomnium spp.</i>
		Disturbed nutrient-poor river bed (dry)	6	<i>Casseopea spp, Dryas integrifolia</i>	<i>Racomitrium cf. lanuginosum</i>

Table 2. The effect of watering on active layer, water content, NDVI and GPP of *Racomitrium* species.

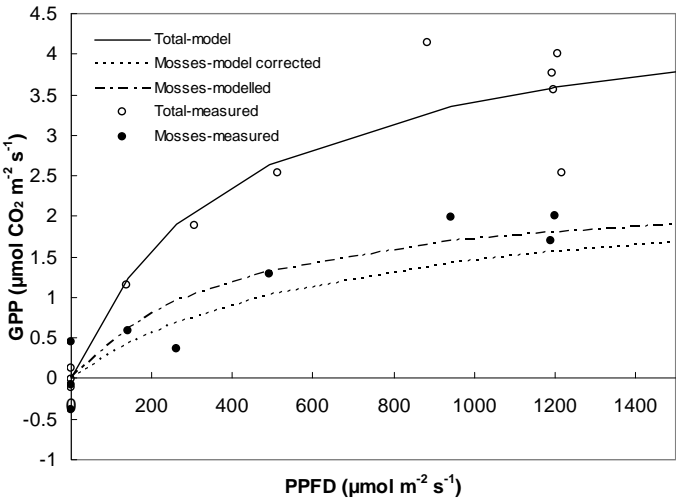
	Active layer cm)	Water content (%)	NDVI	GPP ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
Before watering	0.2	19	0.43	0.16
After watering	0.5	281	0.54	1.35

Figure legends

- Figure 1. An example of a relationship between *PPFD* and gross primary productivity (measured and modelled) of a *Betula* and *Hylocomium* dominated plot in Abisko (model according to Eqn. 3): of the whole ecosystem (black line), of mosses after removal of the plants (dash-dotted line), and of mosses after light extinction correction (dotted line) (a); moss P_{\max} relative to whole system P_{\max} versus LAI of vascular plants (b) and the relationship between LAI of vascular plants and P_{\max} corrected for moss contribution (grey line) and not corrected for moss contribution (black line) (c)
- Figure 2. Relationships between NDVI and the GPP-model parameters for ecosystem (open dots) and moss level (black dots), between NDVI and measured GPP_{\max} (a) and NDVI and measured initial LUE (b)
- Figure 3. Relationship between dark respiration (R_e) at ecosystem level and soil temperature at 5 cm depth.
- Figure 4. Relationship between *PPFD* and water fluxes of a *Betula* and *Aulacomnium* dominated plot in Abisko: of the whole ecosystem (black line), of mosses after removal of the plants (dash-dotted line), and of mosses after light extinction correction (dotted line) (a), and the relationship between LAI of vascular plants and the contribution of mosses to water fluxes (b).
- Figure 5. Relationships between moss and soil evaporation in the dark and the temperature of the moss layer (a) between c_{mosses} and of moss water content (b) and between c_{total} and LAI of vascular plants (solid line) and c_{vascular} and LAI of vascular plants (grey line) (c)
- Figure 6. Asymptotic relationship of the green moss layer, which is assumed to be the

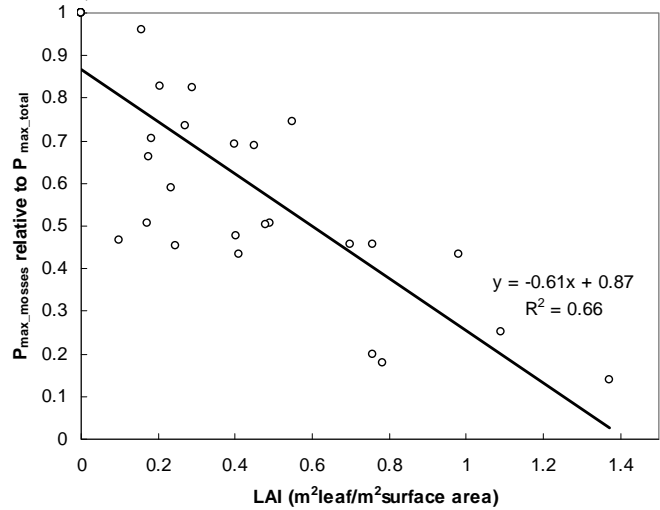
active photosynthesizing layer, and NDVI

1 **Figure 1a)**



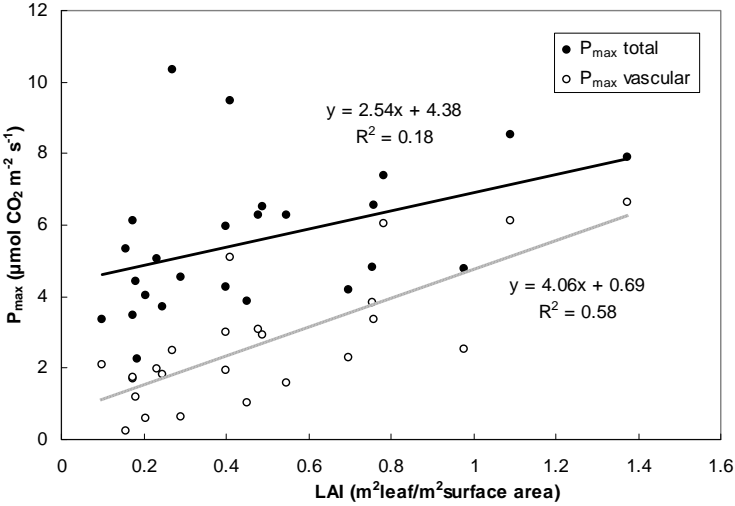
2
3

4 **Figure 1b)**



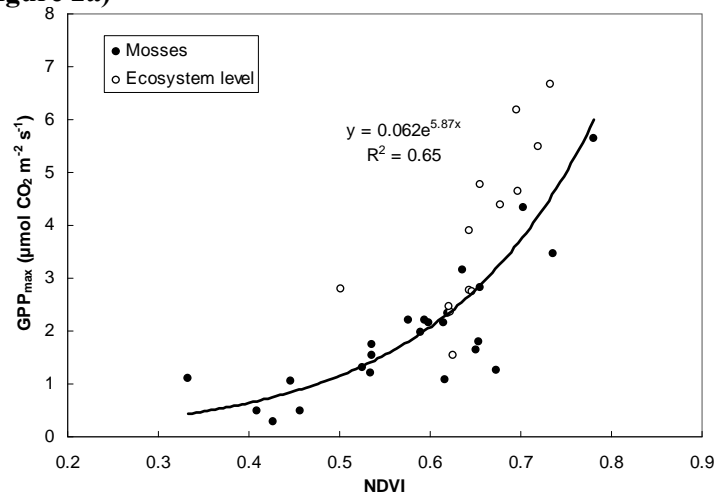
5
6

7 **Figure 1c)**



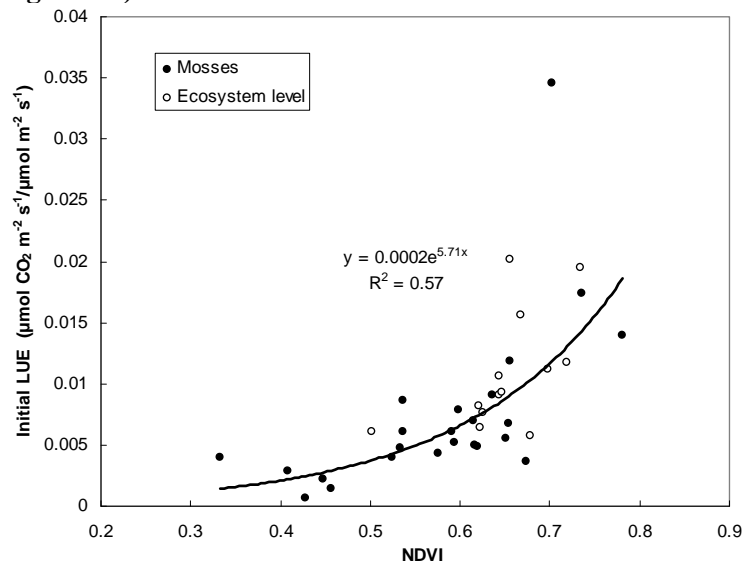
8
9

10 **Figure 2a)**



11
12

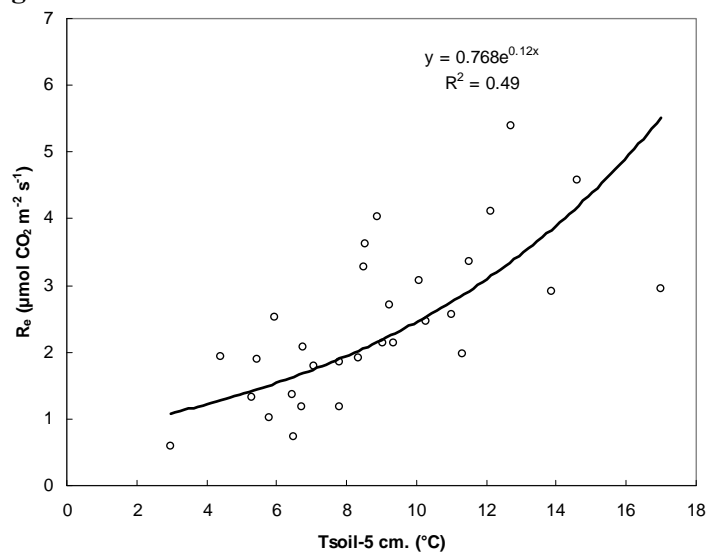
13 **Figure 2b)**



14

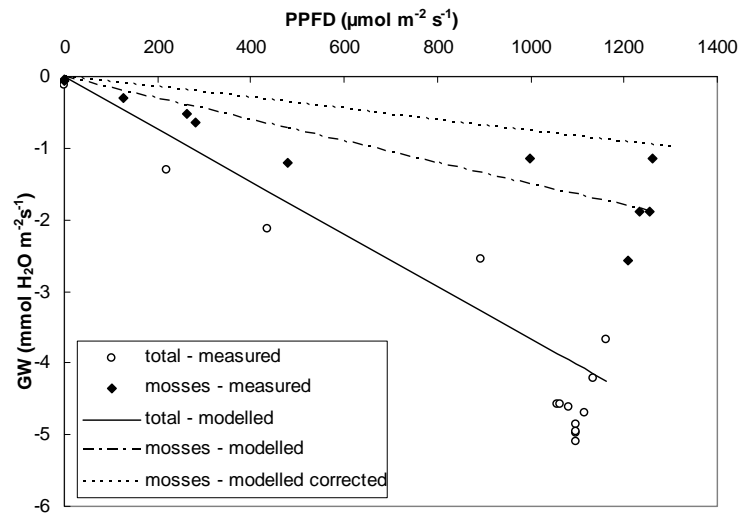
15

16 **Figure 3**



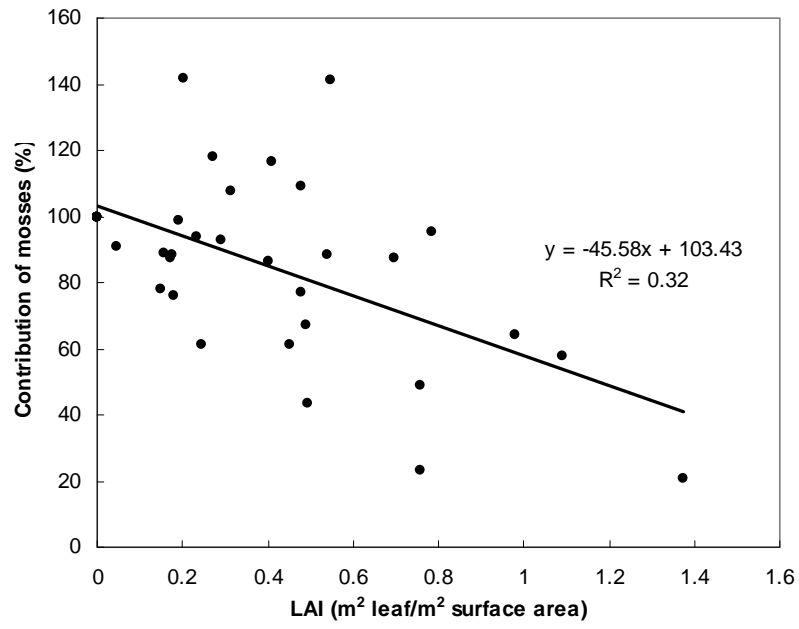
17
18

19 **Figure 4a)**



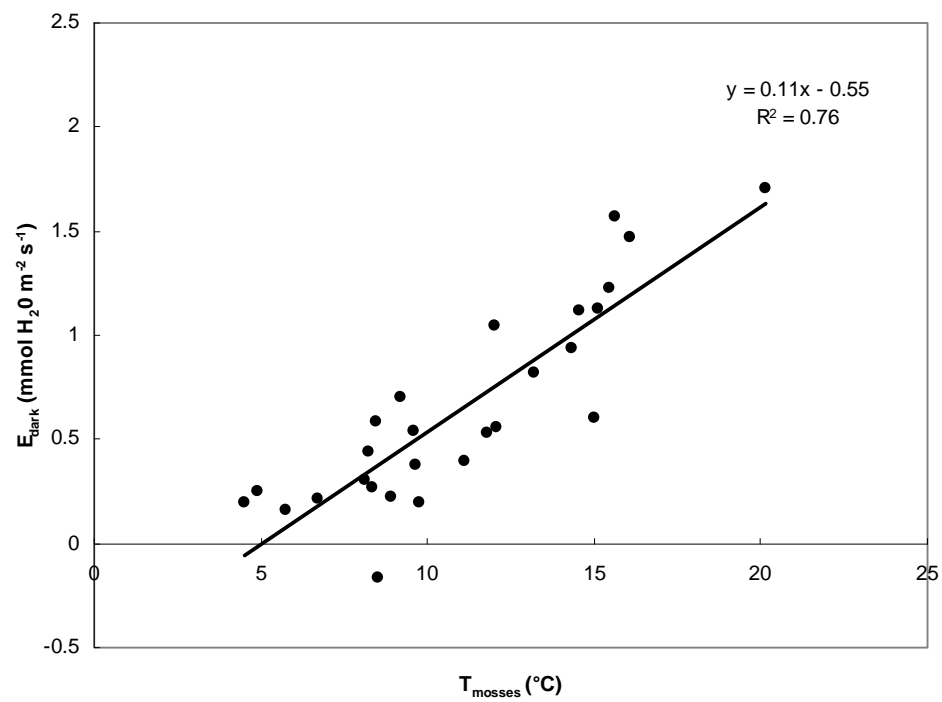
20
21

22 **Figure 4b)**



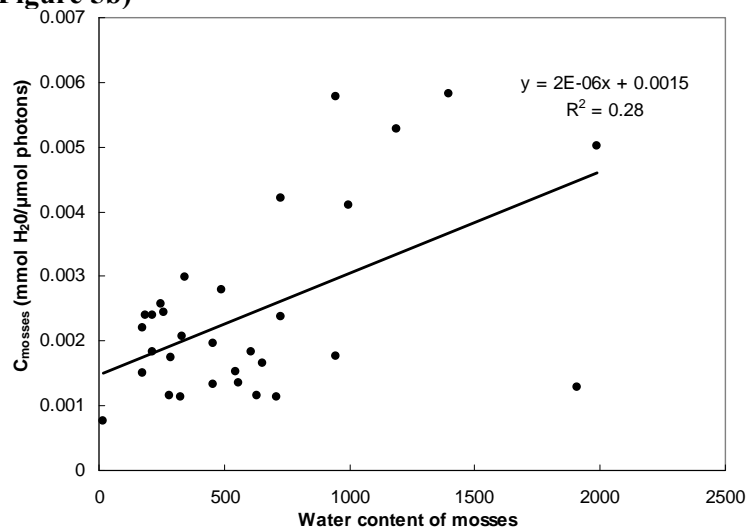
23
24

25 **Figure 5a)**



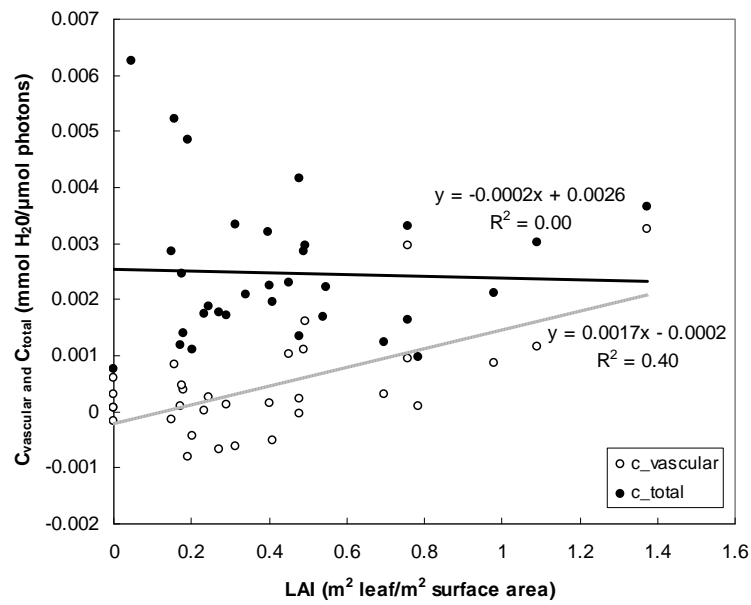
26
27

28 **Figure 5b)**



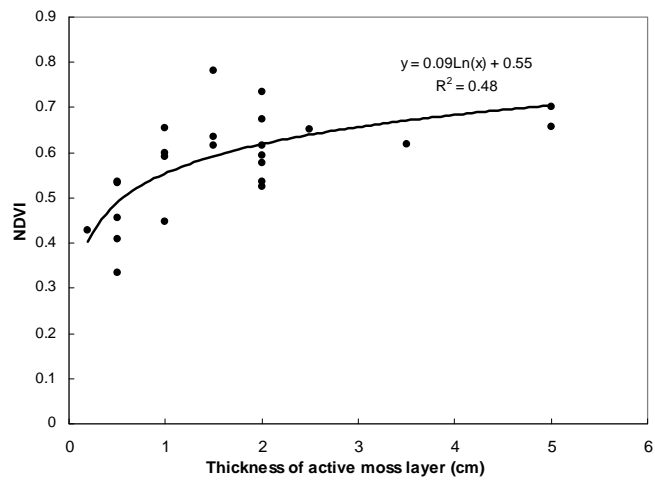
29
30

31 **Figure 5c)**



32
33

34 **Figure 6**



35
36